Check List the journal of biodiversity data

LIST OF SPECIES

Check List 14 (5): 877–891
https://doi.org/10.15560/14.5.877

PENSOFT

Non-volant mammal inventory of Cusuco National Park, north-west Honduras: reporting the presence of Jaguar, *Panthera onca* (Linnaeus, 1758), and demonstrating the effects of zonal protection on mammalian abundance

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Abstract

Neotropical cloud forests are one of the most biodiverse yet threatened ecosystems with deforestation and hunting creating major problems. We report a non-volant mammal species inventory for Cusuco National Park, Honduras, spanning 2006–2016. Data were collected using 4 methods: tracks and signs, camera trapping, direct sightings and live trapping. Recorded species of conservation importance included Central American red brocket (*Mazama temama* (Kerr, 1792)), Baird's tapir (*Tapirus bairdii* (Gill, 1865)), margay (*Leopardus wiedii* (Schinz, 1821)), and jaguar (*Panthera onca* (Linnaeus, 1758)); the latter recorded for the first time. Cusuco National Park is a site of strategic geographical importance within the Central American jaguar corridor. In total, 43 species were recorded from 26 families. We demonstrate the impact of zonal protection measures with higher mammal abundance recorded in the park's highly protected core compared to the less protected buffer zone. We advise continued monitoring to provide robust time-series of population trends.

Key words

Bushmeat; diversity; *Tapirus bairdii;* brocket; Central America.

Academic editor: William Corrêa Tavares | Received 22 February 2018 | Accepted 11 July 2018 | Published 19 October 2018

Citation: Hoskins HMJ, Burdekin OJ, Dicks K, Slater KY, McCann NP, Jocque M, Castañeda F, Reid N (2018) Non-volant mammal inventory of Cusuco National Park, north-west Honduras: reporting the presence of Jaguar, *Panthera onca* (Linnaeus, 1758), and demonstrating the effects of zonal protection on mammalian abundance. Check List 14 (5): 877–891. https://doi.org/10.15560/14.5.877

Introduction

Neotropical cloud forests form part of the Mesoamerican biodiversity hotspot located within the Panamanian biogeographical realm (Myers et al. 2000). Cloud forest is one of the most threatened ecosystems (Higuera et al. 2012, Rojas-Soto et al. 2012) due to human encroachment, deforestation, forest degradation (e.g. fuel wood collection), hunting (e.g. for bushmeat due to food insecurity, reducing family expenditure, sport or tradition), road construction, and global climate change (Foster 2001, Luna-Vega et al. 2001, Ponce-Reyes et al. 2013)

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compounded by altitudinal isolation (Rojas-Soto et al. 2012).

Neotropical cloud forests are typified by high altitude, high precipitation and regular immersion in cloud (Stadtmüller 1987, Scatena et al. 2010). Parque Nacional Cusuco (hereafter referred to as Cusuco National Park), in north-west Honduras, is a protected high altitude forest within which there are 4 principal habitats; i) tropical lowland dry forest, ii) tropical moist forest, iii) montane (cloud) forest and iv) 'bosque enano' or dwarf forest occurring above 2,000 m a.s.l. Originally granted protected status due to its importance as a water catchment (Mejía 2001), the park is recognized by the International Union for the Conservation of Nature (IUCN) as a Key Biodiversity Area (KBA) due to the overlapping ranges of several globally threatened endemic amphibians (BirdLife International 2017). Cusuco National Park is ranked as the 123rd most irreplaceable site, from over 173,000 protected areas, for the conservation of threatened amphibians, birds and mammals (Le Saout et al. 2013). Furthermore, jaguar (*Panthera onca* (Linnaeus 1758)); an IUCN Red-Listed Near Threatened species with a decreasing population trend (Quigley et al. 2017) has gone unrecorded in Cusuco National Park, which is considered to be an important and critical section of the Central American jaguar corridor (Petracca et al. 2017, Wultsch et al. 2016). Additionally, it has been identified as a regional hotspot and important connection node for Baird's tapir (*Tapirus bairdii* Gill 1865) (Schank et al. 2017), an IUCN Red-Listed Endangered species with a decreasing population trend (Garcìa et al. 2016).

Despite its designation, Cusuco National Park is threatened by illegal logging (particularly in the north and west) and agricultural encroachment due to coffee, cardamom, crop and grassland agriculture. Large mammals in the region are threatened by illegal hunting for bushmeat and sport. Baird's tapir has declined within the park as demonstrated by dramatically decreased encounter rates and apparent range contraction with VORTEX population viability modelling suggesting its imminent local extirpation (McCann et al. 2012). Despite previous research focusing on tapir, there is a paucity of published data on the mammalian community within the park. There is no published species inventory for the region.

Bushmeat hunting is prevalent within the park, yet conservation action can only be effective with accurate data capture and characterization of the biodiversity present and the species that are rare or threatened. Consequently, we report here a species list for Cusuco National Park with the frequency and type of species records.

Methods

Study area. Cusuco National Park (15°32′31″ N, 088° 15′49″ W), is 23,440 ha of protected area (ICF 2015) in Sierra de Omoa of the Merendón mountain range, Cortés, north-west Honduras (Fig. 1). The Sierra de Omoa are isolated by the alluvial Sula valley to the east and Río Chamelecón valley to the south and southeast, the Río Motagua alluvial plain to the west and northwest and the Bahía de Omoa to the north. The park, a mountainous cloud forest region, rises to 2,240 m above sea level, annual precipitation is 2,788 mm, with mean monthly temperatures ranging from 12.9 °C in December to 20.2 °C in April (Fundación Ecologista 1994). During 1994, the Corporación Hondureña de Desarrollo Forestal (COHDEFOR), delineated the management plan of the park into a 'core zone' covering 7,690 ha where agriculture, burning, mining, hunting, construction of roads, houses, or commercial, public and private institutions or any human settlements are not permitted (ICF 1987). This region was surrounded by a 'buffer zone' covering 15,750 ha within which construction of human settlements, excluding those that existed before the implementation of the management plan, are permitted only under license as well as limited livestock grazing, burning, deforestation, mining, fishing, housing and road construction. Subsistence hunting may be permitted in this area but only if a permit is obtained, which requires travelling to San Pedro Sula, the regional administrative capital (a minimum of 4 hours travel away), and requires applicants to be literate, have understanding of the relevant paper work and transport; consequently, bushmeat hunting is unlicensed and, therefore, illegal.

Since 2006, a total of 7 camps (recording stations) have been established throughout Cusuco National Park; Base camp (15°29′47″N, 088°12′43″W), Cantiles (15°30′48″N, 088°14′30″ W), Cortecito (15°31′24″ N, 088°17′19″ W), Danto (15°31′42″ N, 088°16′39″ W), and Guanales (15° 29′19″ N, 088°14′03″ W) in the core zone, and the villages of Buenos Aires (15°29′59″ N, 088°10′46″ W) and Santo Tomas (15°33′42″ N, 088°18′01″ W) in the buffer zone. A transect network was established in 2006 by cutting (with machetes) 4 approximately 2 km line transects radiating out from each camp (approximately 8 km for each of the 7 camps with 28 transects and 56 km in total) along natural features including valley bottoms or ridges that could be relatively easily traversed. Species records for non-volant, terrestrial mammals were collected as part of long-term annual biodiversity monitoring and surveillance by a range of students, supervised by academics and local trackers using a range of methods.

Permits to carry out research were obtained from the Instituto Nacional de Conservación y Desarrollo Forestal Áreas Protegidas y Vida Silvestre (ICF), or National Institute for Conservation and Forestry Development, Protected Areas and Wildlife.

Data Collection. Monitoring and surveillance of small and large mammals was conducted annually during the decade 2006–2016 by Operation Wallacea Ltd (http://opwall.com) as part of their global biodiversity monitoring effort. Camera trap surveys were also conducted independently by Panthera (https://www.panthera.org/) during 3 years (2014–2016) as part of their Jaguar Corridor Initiative.

Small mammals were categorized as those < 2 kg in

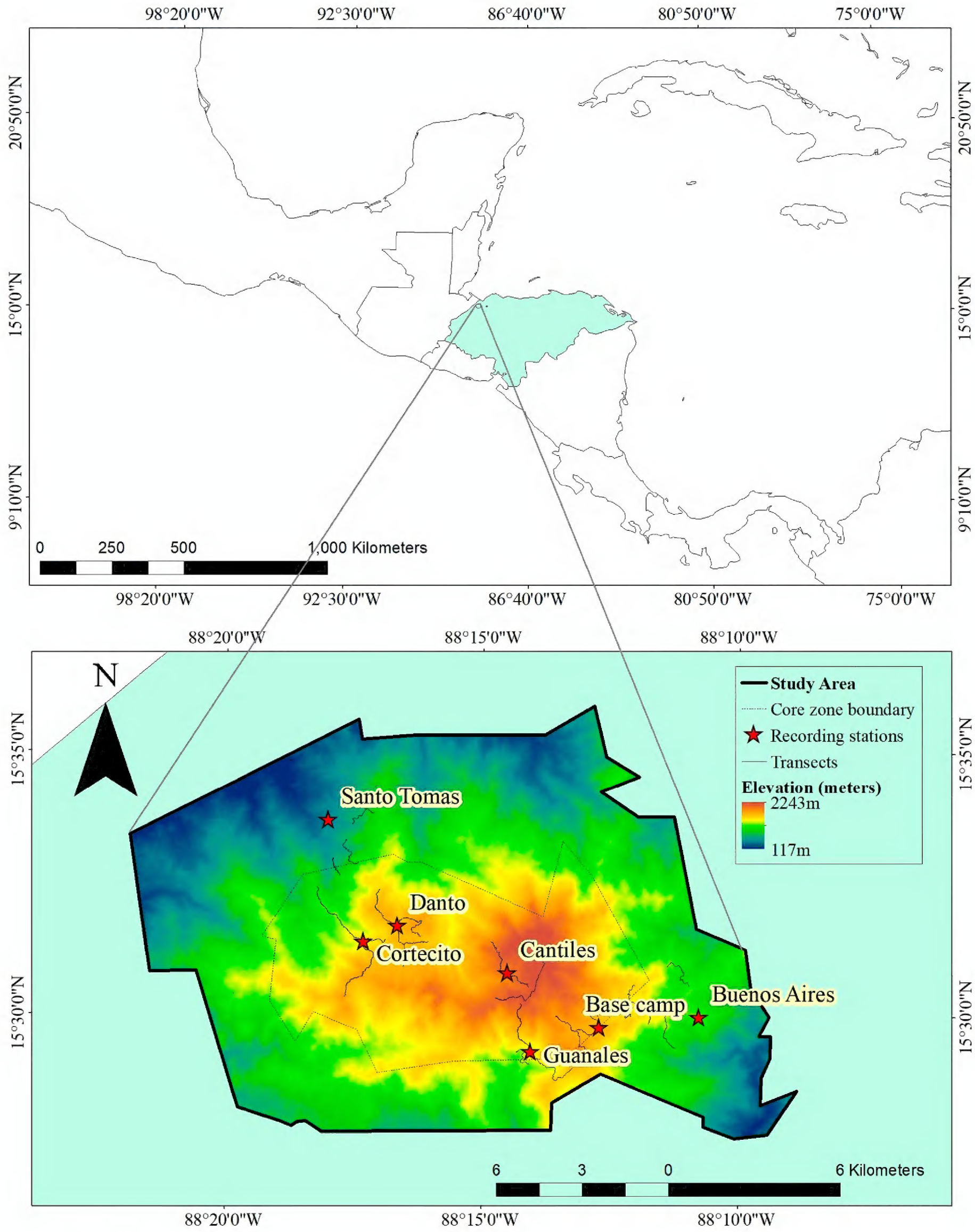

Figure 1. Cusuco National Park, North West Honduras.

body weight. A combination of 6 Freya (320 × 173 × 140 mm) and 6 Sherman traps (508 × 635 × 1651 mm) were set in alternate pairs placed at 10 m intervals for 60 m for a period of 4 consecutive nights and checked daily at sunrise. Traps were baited alternately with a mixture of oats, peanut butter and syrup or tuna. Typically, 2 trap lines were set out on each transect with one placed < 5 m from and parallel to a stream or river (sampling the riparian corridor) and another placed > 150 m from the nearest watercourse (sampling the forest floor) (see Appendix for the list of camps surveyed each year). Surveys were conducted annually between June and August from 2006–2016, totaling 2,376 trap nights in the core zone and 1,272 trap nights in the buffer.

Captures were identified by means of gross external morphology; usually a combination of coloration (including presence of countershading, bicoloration of the tail, etc.), shape and head-body length, tail length,

hind foot length and body weight following Reid (1997, 2009) and Wilson et al. (2017). For the majority, species-specific identification was not contentious as most were well described and commonly found species. However, 2 genera presented particular issues: *Handleyomys* and *Cryptotis*, which have undergone recent taxonomic revision with the description of new cryptic species (e.g. Woodman 2011, 2015, Almendra et al. 2018). Thus, notwithstanding cryptic species, we used gross morphological characters to differentiate captures to species level but, when reporting here, we adopt the use of "cf." to suggest a specimen's species membership.

Cryptotis presented particular problems as many shrew species are indistinguishable by external morphology, with a number of cryptic species being described recently (Woodman 2011, 2015). Thus, a small number of voucher specimens were taken by lethal sampling and lodged with the Royal Museum of Scotland, Edinburgh. Tissue samples were extracted from 10 individuals (2 of which were long-tailed with a TL = 50–53 mm and the rest short-tailed with a TL = 19–29 mm) indicative of the presence of at least 2 species. DNA was extracted using the Qiagen DNeasy blood and tissue kit following the manufacturer's protocol. The cytochrome B (cytB) locus was amplified using primers MVZ05 (5′ – CGA AGC TTG ATA TGA AAA ACC ATC GTT G) (Smith and Patton 1993) and H15915 (5′ – AAC TGC AGT CAT CTC CGG TTT ACA AGA C) (Irwin et al. 1991). PCR reactions were carried out at a final volume of 20 µL containing 1 × ThermoScientific DreamTaq Green Master Mix (includes 0.2 mM dNTP and 2 mM MgCl2), 0.5 µM each primer and water and 2 µL DNA template. PCR cycling conditions were 95 °C for 2 min, followed by 35 cycles of 95 °C 30 s, 58 °C 30 s, 72 °C 30 s, and a final extension of 72 °C 10 min. Amplified products were cleaned by adding 10 U exonuclease I and 1 U shrimp alkaline phosphatase and incubating at 37 °C for 15 min, then 80 °C for 15 min. Products were Sanger sequenced on an ABI 3730XL genetic analyzer (GATC Biotech, Konstanz, Germany). Geneious v. 7.1 was used to edit the sequences. Samples were checked and cleaned for pseudogene co-amplification (identified in 1 sample with a positive cytB sequence). Sequences were compared to GenBank by carrying out a BLAST search and molecular species identification was confirmed if there was a 99–100% match to voucher specimens of a single species in GenBank.

Large mammals (> 2 kg in body weight) were surveyed annually between June and August 2006–2016, these months fall outside of the rainy season (heaviest rainfall is from October to February; Fundación Ecologista 1994). Any bias that this method introduced due to seasonal activity of mammals was logistically unavoidable. Each line transect was walked in its entirety once or twice during this period (see Appendix for details) and species tracks and signs were recorded and, where possible, identified following Reid (1997, 2009). These diurnal transect surveys began at 8 am after 48 hours of no disturbance. This non-disturbance period was to minimize bias toward nocturnal species created by an early morning start time. Although 3 local trackers were involved throughout this study, their identity varied from year to year due to availability. This was an unavoidable source of potential error due to logistical constraints and the long-term nature of the time-series. Typical walking speed was 1–2 km/h, culminating in a total of 600 km of transect survey in the core and 216 km in the buffer zone. Indirect detections were footprint tracks (a.k.a. spoor), whilst signs were any species-specific markings, for example, scat, distinctive scratch marks or food remains with identifiable tooth marks. Indirect signs also included vocalizations, particularly for arboreal species such as primates. Direct sightings of any species were also recorded but rare.

Additionally, camera traps (Bushnell Trophy Cam HD model 119477) were placed either in pairs or in triplets at locations on each transect approximately 1 km apart (minimum separation along transects was 200 m and maximum was 1.5 km). Paired deployments (2014 only, were part of a pilot study) were placed < 20 m and ca 75 m perpendicular from the transect, whilst triplet deployments (2015–2016) were placed off-trail at < 20 m, ca 150 m and ca 300 m, perpendicular to the transect in an attempt to quantify differences in detection with distance from access trails. Cameras were deployed for ca 29 consecutive nights in 2014 but just 3 consecutive nights during 2015–2016 (all survey effort was approximately equal between cameras within- and between-transects within-years). This decrease in survey effort per session was to increase the number of independent sampling locations as we wanted to minimize problems associated with field of view, theft etc. Cameras were strapped to trees at approximately 30 cm height from the ground at locations where areas were clear from vegetation for a distance of up to 3 m directly in front of the camera. Camera trapping occurred at Buenos Aires during 2014 only and was not conducted at Santo Tomas, there were also occasions where cameras were stolen or malfunctioned (see Appendix for camera numbers each year). In total, 1,043 trap nights occurred in the core zone and 402 trap nights in the buffer zone. Traps were deployed upon completion of line transect surveys to minimize capturing the same individuals on cameras as detected by tracks and signs. Cameras were set to record 20 second videos with a minimum trigger interval of 1 minute. Any videos of the same species recorded within 1 hour were excluded from analyses as they may represent repeat detections.

For the camera trap survey carried out by Panthera, cameras of model Moultrie M-100 and Panthera Cams were used. Cameras were placed on human trails and mountain ridges to maximize the probability of capturing jaguar images. Between 3 and a maximum of 12 cameras were deployed at a time for 30–90 consecutive nights from 2014–2016 during both the dry and rainy season. Cameras were strapped to trees at approximately 30 cm height from the ground and aimed directly at trails. Only

the species not detected by the main Operation Wallacea Ltd., camera trapping surveys have been included here for the purpose of providing a comprehensive species inventory.

Data Analysis We processed camera trap videos manually. For image organization and management, we used the *camtrapR* package (Niedballa et al. 2017) for R (R Core Team 2017) in RStudio (RStudio Team 2015).

We calculated indices of abundance for each survey technique separately for data collected within the core and buffer zones (for the purposes of comparison). For line transect surveys, the number of records were divided by the total kilometers surveyed in each zone and multiplied by 10 to give detections/10 km. For live trapping, we divided the number of records by the total number of trap nights in each zone multiplied by 30 nights to give detections/month for each zone. For camera trapping surveys, we divided the number of records for each zone by the total number of fractional days (to account for time of day at which cameras were deployed/collected) multiplied by 30 to give detections/month within each zone. Standardization of the units allowed direct comparison of detection rates between zones.

We calculated Shannon's Evenness Index for species community composition for small mammals using live trapping data and large mammals using tracks and signs from walked transects using the R package *vegan* (Oksanen et al. 2018). Whittaker rank abundance plots were also created using the same data. Both metrics accounted for the standardization of detection rates. We created Species Accumulation Curves for all small and large mammals pooled across survey methods to determine if our species inventory was nearing asymptote.

To assess differences in detection rates between the core and buffer zones, we conducted Wilcoxon rank sum tests on indices of abundance on data from each survey method separately. These analyses were carried out in RStudio and plotted using the package *ggplot2* (Wickham 2009).

Results

Species Accumulation Curves for large mammals reached asymptote in 2014; 9 years after surveys began (Fig. 2A), not withstanding the detection of jaguar during 2016. Small mammal data have yet to reach asymptote increasing with a decelerating rate of discovery throughout the times-series with the addition of new species in virtually every year of survey.

The small mammal community (21 species) was unevenly structured being dominated by 2 species (Fig. 2B; Table 1), the Mexican deer mouse (*Peromyscus mexicanus* (Saussure, 1860)) with 25 records/month and Desmarest's spiny pocket mouse (*Heteromys desmarestianus* Gray, 1868) with 20 records/month. Of the 3 candidate *Handleyomys* species possibly present at the site, 2 were tentatively identified as *Handleyomys* cf. *rostratus* and *Handleyomys* cf. *alfaroi* (Table 1); further work including molecular genetic analyses may be required to confirm these identities.

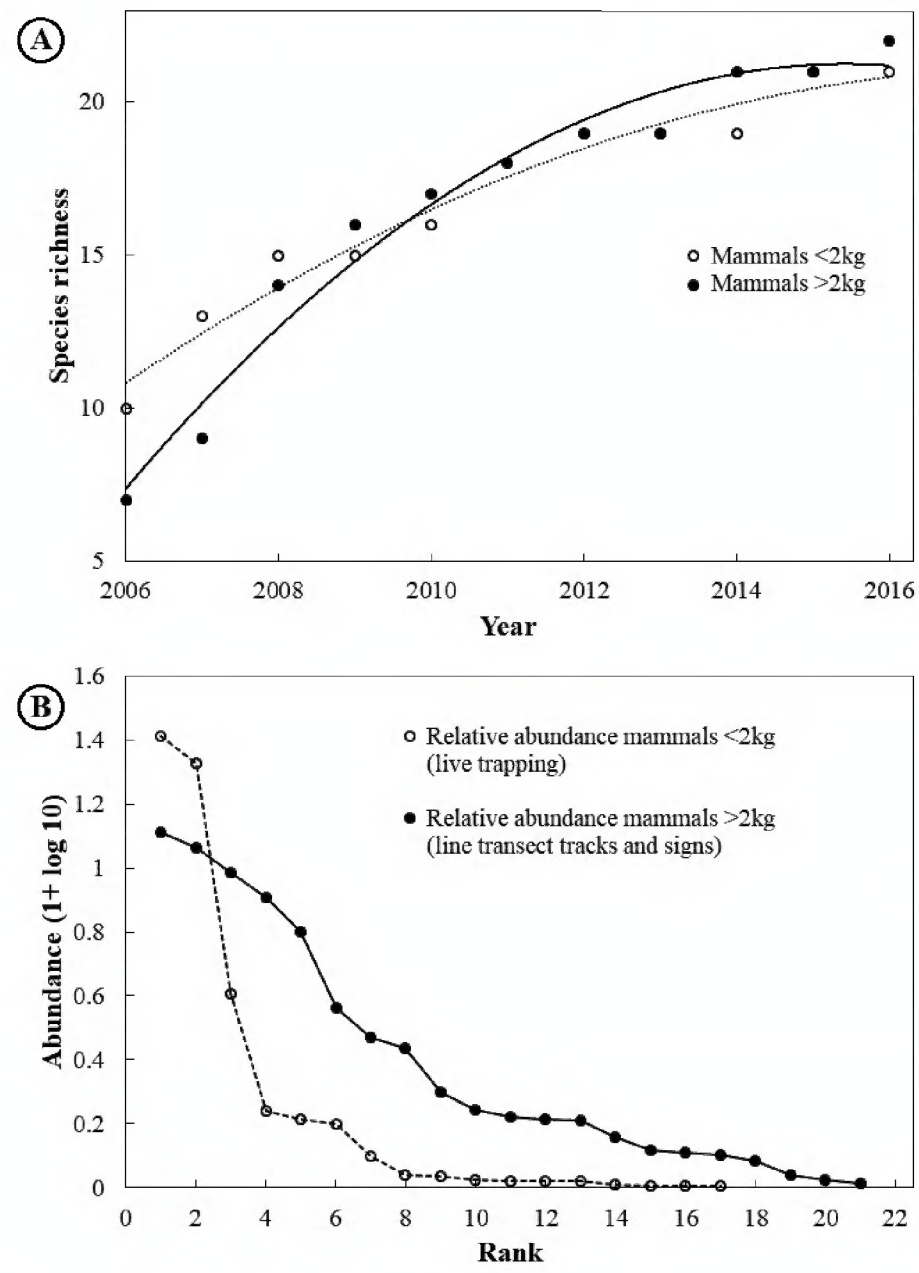

Figure 2. A. Species accumulation curves for small mammal species detections (Note: small mammals were not surveyed in 2011). **B.** Whittaker rank abundance plot exhibiting species richness from 2 survey methods.

The large mammal community consisted of 22 species with a more even structure than the small mammal community, i.e. not dominated by a few common species (Fig. 2B, Table 2). The small mammal community had a Shannon index = 1.14 compared to that of the large mammal community with a Shannon index = 2.25 (further confirming that the small mammal community was skewed by a few hyperdominant species). Of the large mammals, the most commonly detected species included Central American red brocket deer (*Mazama temama* (Kerr, 1792)) with 12 records/10 km, white-nosed coati (*Nasua narica* (Linnaeus, 1766)) with 11 records/10 km, Baird's tapir with 9 records/10 km and spotted paca (*Cuniculus paca* (Linnaeus, 1766)) with 7 records/10 km surveyed. Species of conservation importance included the Data Deficient Central American red brocket deer, the Near Threatened jaguar and margay (*Leopardus wiedii* (Schinz, 1821)) and the Endangered Baird's tapir (Fig. 3). Twelve other species recorded on camera traps are shown in Figure 3. Jaguar had previously gone unrecorded in Cusuco National Park and its detection (Table 2; Fig. 3) is strategically and geographically important within the Central American jaguar corridor.

Standardized relative indices of mammal abundance

Table 1. Non-volant (small) mammals < 2 kg. IUCN Red List code: DD= Data Deficient, LC = Least Concern (IUCN statuses extracted from http://www.iucnredlist.org, version 2016.3). †: there have been identifications to species level (*Sciurus variegatoides* and *Sciurus deppei*) in the study area by the author MJ, however, most were recorded just to genus only. ‡: Detection type: LT = captures/month, TS = tracks and/or signs/10 km, DS = direct sighting/10 km, CT = Camera trap detection/month, PCT = Panthera camera trap (index of abundance not included).

Species recorded	Common name	IUCN status	Core zone index of abundance	Buffer zone index of abundance	Detection type‡
RODENTIA					
Cricetidae					
Handleyomys cf. rostratus (Merriam, 1901)	Long-nosed rice rat	LC	0.03	0.07	LT
Tylomys nudicaudus Peters, 1866	Peters's climbing rat	LC	0.04	0.02	LT
Nyctomys sumichrasti (Saussure, 1860)	Vesper rat	LC	0.05	0	LT
Peromyscus mexicanus (Saussure, 1860)	Mexican deer mouse	LC	13.25	11.51	LT
Handleyomys cf. *alfaroi* (J.A. Allen, 1891)	Alfaro's rice rat	LC	0.49	0.09	LT
Oligoryzomys fulvescens (Saussure, 1860)	Fulvous pygmy rice rat	LC	0.01	0	LT
Reithrodontomys cf. *gracilis* J.A. Allen & Chapman, 1897	Slender harvest mouse	LC	0.05	0.21	LT
Scotinomys teguina (Alston, 1877)	Short-tailed singing mouse	LC	1.25	1.79	LT
Erethizontidae					
Sphiggurus mexicanus (Kerr, 1792)	Mexican hairy dwarf porcupine	LC	0.02	0.05	TS (DS)
Geomyidae					
Orthogeomys sp.	Pocket gopher	LC	0.18	0.14	TS
Heteromyidae					
Heteromys desmarestianus Gray, 1868	Desmarest's spiny pocket mouse	LC	14.53	5.61	LT
Muridae					
Mus musculus Linnaeus, 1758	House mouse	LC	0	0.05	LT
Sciuridae†					
Sciurus sp.	Squirrel	LC	2.39	1.57	CT
DIDELPHIMORPHIA					
Didelphidae					
Didelphis marsupialis Linnaeus, 1758	Black-eared opossum	LC	0.27	0.47	LT
Marmosa mexicana Merriam, 1897	Mexican mouse opossum	LC	0.28	0.35	LT
LAGOMORPHA					
Leporidae					
Sylvilagus gabbi gabbi (J.A. Allen, 1877)	Tapeti rabbit	LC	0.01	0	LT
CARNIVORA					
Mustelidae					
Mustela frenata Lichtenstein, 1831	Long-tailed weasel	LC	0.05 0.03	0 0.15	LT CT
Procyonidae					
Bassariscus sumichrasti (Saussure, 1860)	Cacomistle	LC	NA	NA	PCT
EULIPOTYPHLA					
Soricidae					
Cryptotis mccarthyi Woodman, 2015	Omoa broad-clawed shrew	DD	NA	NA	LT
Cryptotis merriami Choate, 1970	Merriam's small-eared shrew	LC	NA	NA	LT
Cryptotis orophila (J.A. Allen, 1895)	Central American least shrew	DD	NA	NA	LT

did not differ significantly between the core than buffer zones (due to the high prevalence of zero detections and wide variation in detection at sites within each zone) but were consistently higher within the core and buffer zone, specifically, mammal tracks and signs on line transect surveys were 30% higher (W = 219.5, P =0.79), camera trap detections were 46% higher (W = 127, P =0.56) and small mammal live trapping capture rates were 33% higher (W= 128, P= 0.58) within the core compared to buffer zone (Fig. 4).

Identification

Species accounts of uncommon species (< 10 records) or those where identification required some further explanation are included below for reference with the exception of the house mouse (*Mus musculus*) as it is sufficiently recognized globally.

Oligoryzomys fulvescens (Saussure, 1860)

Material examined. Honduras, Cortés, Cusuco National Park, 15°31′24″ N, 088°17′19″ W**,** Neil Reid, 2012, Table 1.

Longer tail than other Central American mice of similar size. The differences in ratio of toe lengths as well as differences in upper incisors with similar harvest mouse species (Reid 2009) were used to identify this species.

Sphiggurus mexicanus (Kerr, 1792)

Table 2. Non-volant (medium-sized to large) mammals > 2 kg. Station codes: BA = Buenos Aires, BC = base camp, CA = Cantiles, CO = Cortecito, CP = Capuca, DA = Danto, GU = Guanales, ST = Santo Tomas. IUCN Red List codes: DD = Data deficient, LC = Least Concern, NT = Near Threatened and EN = Endangered (IUCN statuses extracted from http://www.iucnredlist.org, version 2016.3). †: Index of abundance not stated for those records provided by Panthera. ‡: Detection type: LT = captures/month, TS = tracks and signs/10 km, DS = direct sighting/10 km, CT = Camera trap detections/month, PCT = Panthera camera trap.

Species recorded	Common name	IUCN status	Core zone index of abundance†	Buffer zone index of abundance	Type of detection‡
PRIMATES					
Atelidae					
Alouatta palliata (Gray, 1849)	Mantled howler monkey	LC	1.5	0.46	TS (DS)
CARNIVORA					
Canidae					
Urocyon cinereoargenteus (Schreber, 1775)	Gray fox	LC	0.13	0.09	TS
Felidae					
Leopardus wiedii (Schinz, 1821)	Margay	NT	0.04	0	TS
			0.26	0.22	CT
Leopardus pardalis (Linnaeus, 1758)	Ocelot	LC	0.39	0.28	TS
Herpailurus yagouaroundi (É. Geoffroy-Hilaire, 1803)	Jaguarundi	LC	0.13	0.14	TS
			0.03	0	CT
Panthera onca Linnaeus, 1758	Jaguar	NT	NA		PCT
Mephitidae					
Conepatus semistriatus (Boddaert, 1785)	Striped hog-nosed skunk	LC	0.25	0.74	TS (DS)
Mustelidae					
Eira barbara (Linnaeus, 1758)	Tayra	LC	0.11	0.19	TS
			0.03	0.08	CT
Galictis vittata (Schreber, 1776)	Greater grison	LC	NA	NA	PCT
Procyonidae					
Potos flavus (Schreber, 1774)	Kinkajou	LC	0.39	0.23	TS
			0.06	0.15	CT
Nasua narica (Linnaeus, 1766)	White-nosed coati	LC	6.09	4.44	TS
			0.72	0.08	CT
Procyon lotor (Linnaeus, 1758)	Northern raccoon	LC	0.30	0.14	TS
CETARTIODACTYLA					
Cervidae					
Mazama temama (Kerr, 1792)	Central American red brocket	DD	6.36	5.56	TS
			0.63	0.60	CT
Odocoileus virginianus (Zimmermann, 1780)	White-tailed deer	LC	0.86	0.88	TS
			0	0.15	CT
Tayassuidae					
Pecari tajacu (Linnaeus, 1758)	Collared peccary	LC	0.43	0.32	TS
			0.58	0	CT
RODENTIA					
Cuniculidae					
Cuniculus paca (Linnaeus, 1766)	Spotted paca	LC	3.97	3.10	TS
			1.73	0.22	CT
Dasyproctida					
Dasyprocta punctata (Gray, 1842)	Agouti	LC	0.45	0.19	TS
			0.06	0.08	CT
CINGULATA					
Chlamyphoridae					
Cabassous centralis (Miller, 1899)	Northern naked-tailed Armadillo	DD	NA	NA	PCT
Dasypodidae					
Dasypus novemcinctus Linnaeus, 1758	Nine-banded armadillo	LC	3.22	2.08	TS
			0.09	0.08	CT
DIDELPHIMORPHIA					
Didelphidae					
Didelphis virginiana (Kerr, 1792)	Virginia opossum	LC	0.03	0.05	LT
			1.54	1.11	TS
			0.43	0.60	CT
PILOSA					
Myrmecophagidae					
Tamandua mexicana (Saussure, 1860)	Northern tamandua	LC	0.01	0	LT
PERISSODACTYLA					
Tapiridae					
Tapirus bairdii (Gill, 1865)	Baird's tapir	EN	7.22	1.44	TS
			0.17	0	CT

Figure 3. Photographs of key species detections including: (**A**) Data Deficient Central American red brocket deer (*Mazama temama*), (**B**) Near Threatened margay (*Leopardus wiedii*), and (**C**) Endangered Baird's tapir (*Tapirus bairdii*). Further photographs of species detected on camera traps including: (**D**) White-nosed coati (*Nasua narica*), (**E**) Jaguarundi (*Herpailurus yagouaroundi*), (**F**) Collared peccary (*Pecari tajacu*), (**G**) Paca (*Cuniculus paca*), (**H**) Kinkajou (*Potos flavus*), (**I**) White-tailed deer (*Odocoileus virginianus*), (**J**) Agouti (*Dasyprocta punctata*), (**K**) Tayra (*Eira barbara*), (**L**) Mexican hairy dwarf porcupine (*Sphiggurus mexicanus*) [photo credit: Katie Rapson], (**M**) Cacomistle (*Bassariscus sumichrasti*) [Photo credit: Panthera Honduras], (**N**) Greater grison (*Galictis vittata*) [photo credit: Panthera Honduras], (**O**) Northern naked-tailed armadillo (*Cabassous centralis*) [photo credit: Panthera Honduras], (**P**) Jaguar (*Panthera onca*) caught by camera trap at 2,200 m a.s.l. [photo credit: Panthera Honduras], (**Q**) Tapeti rabbit (*Sylvilagus gabbi gabbi*) when removed from a trap in 2010 [photo credit: Rachael Forster], (**R**) hunter carrying weapon stands in front of camera trap.

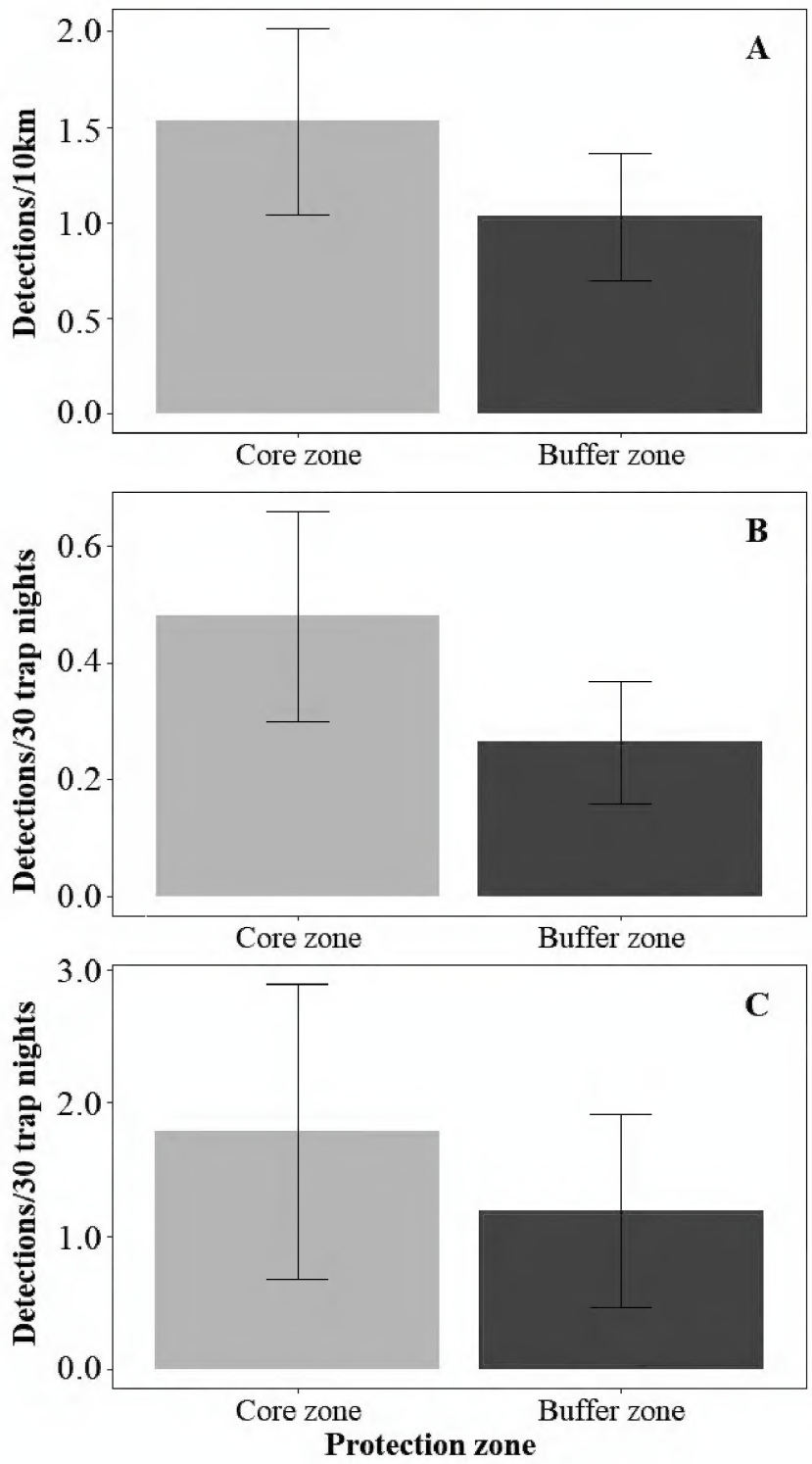

Figure 4. A. Relative abundance of tracks and signs on line transects surveys/10 km in the core vs buffer. **B.** Relative camera trap detections/month. **C.** Relative capture rate by live trapping/month. All 3 plots include standard error bars.

Material examined. Honduras, Cortés, Cusuco National Park, 15°30′48″ N, 088°14′30″ W, Katy Wilson, 2008, Table 2, Figure 3L.

The only species of porcupine found in Honduras (Reid 2009).

Bassariscus sumichrasti (Saussure, 1860)

Material examined. Honduras, Cortés, Cusuco National Park, Franklin Castañeda, 2014, Table 2; Figure 3M.

From camera trap footage it was distinguished from other similar species due to its bushier and very clearly banded tail (Reid 2009).

Tylomys nudicaudus Peters, 1866

Material examined. Honduras, Cortés, Cusuco National Park, 15°31′24″ N, 088°17′19″ W, David Beaune, 2008, Table 1.

Distinguished from other species of its genus by its geographic range (Reid 2009), it differed from other similar species due to a white-tipped tail (Reid 2009).

Nyctomys sumichrasti (Saussure, 1860)

Material examined. Honduras, Cortés, Cusuco National Park, Dario Rivera, 2007, 15°30′48″ N, 088°14′30″ W, Table 1.

Geographically distant to similar species (Reid 2009).

Reithrodontomys gracilis J.A. Allen & Chapman, 1897

Material examined. Honduras, Cortés, Cusuco National Park, 15°31′24″ N, 088°17′19″ W, Dario Rivera, 2007, Table 1.

Small size distinguished it from other very similar species (Reid 2009).

Mustela frenata (Lichtenstein, 1831)

Material examined. Honduras, Cortés, Cusuco National Park, 15°29′19″ N, 088°14′03″ W, Dario Rivera, 2007, Table 1.

Elongated body and narrow tail, easily distinguishable from similar species due to much smaller size and clearly different tail to squirrel species (Reid 2009; screen-grabs of camera trap recordings from 2015 or 2016 have not been included as they are not clear as still images).

Tamandua mexicana (Saussure, 1860)

Material examined. Honduras, Cortés, Cusuco National Park, 15°30′48″ N, 088°14′30″ W, Dario Rivera, 2007, Table 2.

Nothing else in the region with which it may have been mistaken (Reid 2009).

Galictis vittata (Schreber, 1776)

Material examined. Honduras, Cortés, Cusuco National Park, Franklin Castañeda, 2014, Table 2; Figure 3N.

The gray color distinguishes this species easily from other, similar species (Reid 2009).

Cabassous centralis (Miller, 1899)

Material examined. Honduras, Cortés, Cusuco National Park, Franklin Castañeda, 2014, Table 2; Figure 3O.

Flatter body shape than that of *Dasypus novemcinctus*, with a shorter, less robust tail (Reid 2009).

Panthera onca (Linnaeus, 1758)

Material examined. Honduras, Cortés, Cusuco National Park, Franklin Castañeda, 2016, Table 2; Figure 3P.

Shape and markings are unmistakable even with other spotted cat species found in the area (Reid 2009).

Sylvilagus gabbi gabbi (J.A. Allen, 1877)

Material examined. Honduras, Cortés, Cusuco National Park, 15°29′47″ N, 088°12′43″ W, Rachael Forster, 2010, Table 1, Figure 3Q.

The only lagomorph whose range falls across Cusuco

National Park. Figure 3Q shows color patterns which were considered along with size (Reid 2009). Originally described as *Sylvilagus brasiliensis* (Linnaeus, 1758), but taxonomic work has led to its reclassification as *S. gabbi* with those in the study area being subspecies *gabbi* (Allen 1877, Ruedas and Salazar-Bravo 2007).

***Handleyomys alfaroi* (J.A. Allen 1891)**

Material examined. Honduras, Cortés, Cusuco National Park, 15°29′47″ N, 088°12′43″ W, Rachael Forster, 2010, Table 1.

The genus *Handleyomys*, notwithstanding undescribed cryptic species, currently contains 8 described species: *H. chapmani, H. fuscatus, H. intectus, H. melanotis* and *H. rhabdops*, but only 3—*H. alfaroi, H. rostratus* and *H. saturatior*—have ranges that include any part of Honduras and only 2 (*H. alfaroi* and *H. rostratus*) have ranges which included Cusuco National Park (both IUCN range data and Wilson, Lacher and Mittermeier 2017).

Handleyomys alfaroi and *H. saturatior* could conceivably be confused due to their similar body size (HB 90–106 mm and 90–103 mm respectively) but their tails are fairly diagnostic with the former having a shorter tail (89–101mm) than the latter (105–122 mm). Additionally, the former has a lighter coat color (dull yellow-brown) compared to the latter (dark brown very heavily mixed with black).

***Handleyomys rostratus* (Merriam, 1901)**

Material examined. Honduras, Cortés, Cusuco National Park, 15°29′47″ N, 088°12′43″ W, Neil Reid, Table 1.

Following the above, this species is notably larger than the other 2 species of the genus found in Honduras (HB 100–140mm) and distinctly colored, being lighter reddish brown with a white venter and well-defined countershading absent from the other 2 candidate species.

***Cryptotis merriami* Choate, 1970**

Material examined. Honduras, Cortés, Cusuco National Park, 15°29′47.1″ N, 088°12′42.7″ W, Neil Reid, 2012, NMS.Z.2018.80.6, Tables 1, 3, Figure 5.

***Cryptotis orophilus* (J.A. Allen, 1895)**

Material examined. Honduras, Cortés, Cusuco National Park, 15°29′40.8″ N, 088°12′48.1″ W, Neil Reid, 2015, NMS.Z.2018.80.3, Tables 1, 3; Figure 5.

***Cryptotis mccarthyi* Woodman, 2015**

Material examined. Honduras, Cortés, Cusuco National Park, 15°31′11.5″ N, 088°13′55.0″ W, Neil Reid, 2015, NMS.Z.2018.80.4, Tables 1, 3, Figure 5.

Seven out of the 10 *Cryptotis* specimens taken by lethal sampling had successfully amplified DNA and were sequenced for the gene CytB. For all sequences, a greater than 99% species match could be made to voucher specimens sequenced by Baird et al. (2018) from specimens collected in Honduras (Table 3). Of those described as short-tailed, 2 species were identified: *C. merriami* and *C. orophilus*, whilst those described as long-tailed were identified as *C. mccarthyi* (Table 1, Fig. 5).

Four species were detected by indirect methods only. Local trackers identified ocelot (*Leopardus pardalis* Linnaeus 1758) using tracks and feces, Northern raccoon (*Procyon lotor* (Linnaeus, 1758)) and Gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)) using tracks and evidence of food and gopher (*Orthogeomys* sp.) by means of burrows and digging spoil.

Sixteen species whose IUCN range polygons included Cusuco National Park went undetected (Table 4). Notable non-detections included Geoffroy's spider monkey (*Ateles geoffroyi* Kuhl, 1820), puma (*Puma concolor* (Linnaeus, 1771)) and giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758). The park falls within the IUCN range polygon for the Neotropical river otter (*Lontra longicaudis (*Olfers, 1818)), but this species was excluded from Table 4 due to the unsuitability of high altitude habitats i.e. all streams and rivers within the park are small (< 3 m wide) and fishless (confirmed by electrofishing) as they are above impassable waterfalls.

Discussion

Cusuco National Park has previously been considered an important Protected Area (Le Saout et al. 2013), most notably for Baird's tapir, but also strategically positioned within the Central American jaguar corridor despite no previous species records from the region (Petracca et al. 2017, Wultsch et al. 2016, Schank et al. 2017). This study

Table 3. Shrew species identification matches for seven *Cryptotis* specimens using CytB sequencing. Specimens are available at the Royal Museum of Scotland, Edinburgh.

Specimen no.	Species match on GenBank	% pairwise identity	Length of pairwise match (bp)	GenBank accession number of best match
08	*C. merriami*	99.7%	906	MF158110
12	*C. merriami*	99.9%	912	MF158112
13	*C. orophilus*	99.5%	1070	MF158113
18*	*C. maccarthyi*	100.0%	497	MF158096
22	*C. merriami*	99.8%	1117	MF158108
23	*C. merriami*	100.0%	911	MF158110
24	*C. merriami*	99.4%	837	MF158110

* Mixed sequence – sequence match carried out after excluding the pseudogene.

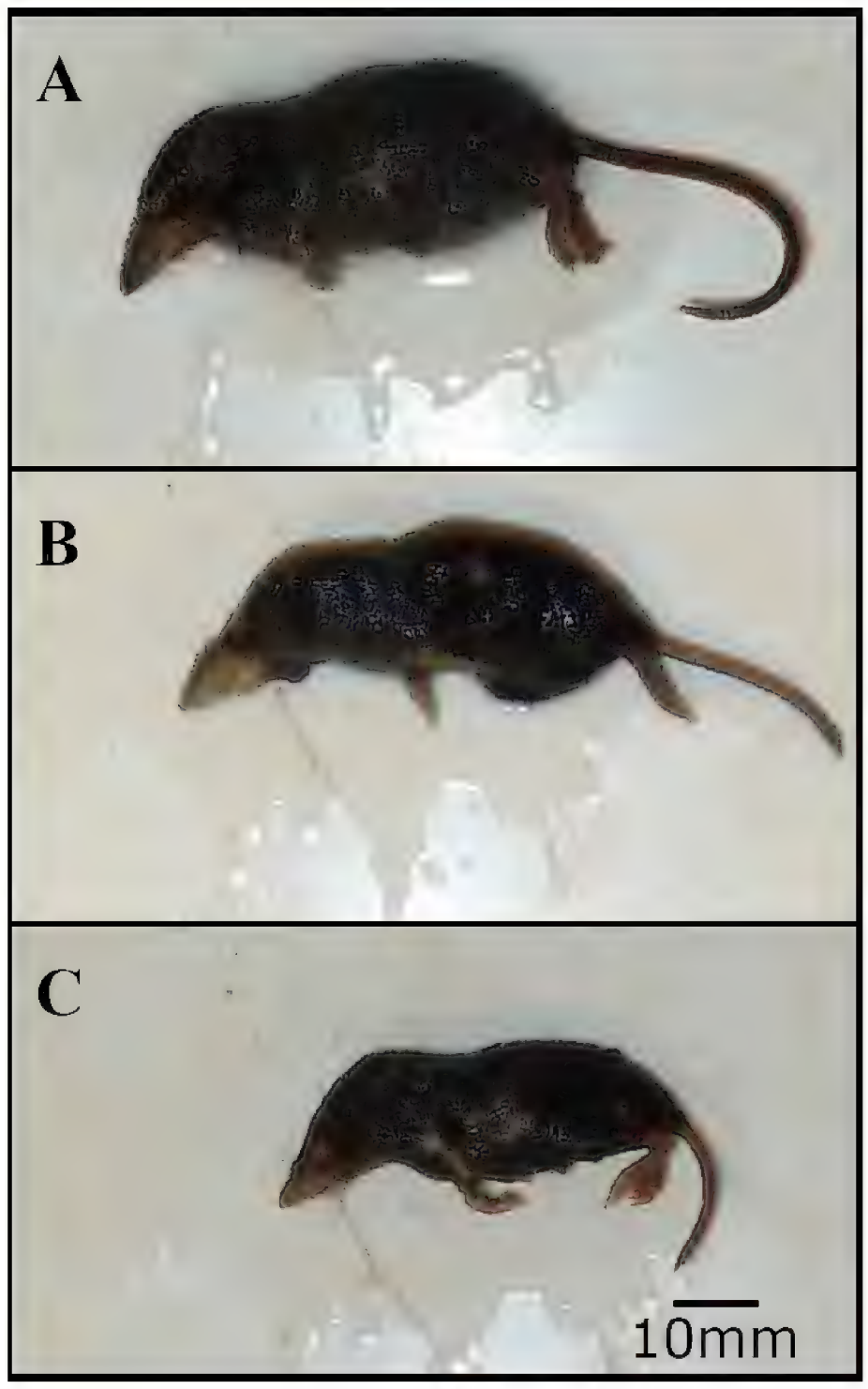

Figure 5. Three example specimens of (**A**) *Cryptotis mccarthyi* (TL = 50mm), (**B**) *C. merriami* (TL = 27–29 mm) and (**C**) *C. orophilus* (TL = 21mm) identified using molecular genetic analysis of CytB sequences.

represents the first comprehensive species inventory for the park and we confirm the presence of jaguar for the first time. Cusuco National Park lies close to the city of San Pedro Sula (Fig. 1) and is highly vulnerable to human disturbance, highlighting the importance of conservation action in the region to protect its diverse mammal fauna.

A camera trapping species inventory from Río Plátano Biosphere Reserve, Honduras (Gonthier and Castañeda 2013) suggests similar species richness to Cusuco National Park. Detection of 79% of expected meso-to-large mammals within Cusuco National Park is comparable to other surveys of similar sized species in the Neotropics (Tobler et al. 2008, Cove et al. 2013). Moreover, the asymptote for our large mammal list suggests a near complete species list whilst increases in small mammals may suggest that further species remain to be described; this is most notable for cryptic species (as in the *Cryptotis* shrews identified here) which require molecular genetic methods.

Indices of relative abundance accounted for survey effort based upon either distance (i.e. for line transects) or duration (i.e. for camera and live trapping). Nevertheless, species-specific detections may have been subject to sources of methodological error or bias as some species may be more easily detected using certain methods, for example, Baird's tapir may leave abundant, long-lasting tracks and signs due to their weight compared to smaller, lighter-footed common species such as paca.

Cusuco National Park has zonal protection with mammal abundances greater within the core zone, which has greater protected status, than within the buffer zone—vulnerable to some level of disturbance and within which there are a number of villages including Buenos Aires and Santo Tomas. Disturbance of intact forest includes fuel wood collection and hunting by people. Hunting platforms (horizontal beams lashed between 2 trees approximately 3 m above ground level on which hunters can perch at dawn and dusk) are regularly encountered throughout the park including within the core zone (pers. obs.), suggesting that some level of human impact may have already occurred within the most pristine areas. Hunters carrying guns were also observed on camera traps (Fig. 3R), whilst distant gunshots have been heard during surveys (pers. obs.). This is in spite of the fact that ongoing deforestation and hunting within Cusuco National Park has resulted in the deployment of army patrols and latterly, park wardens. Nevertheless, zonal differences in mammal abundance suggests that maintaining and enforcing the park's protected status is important. Other studies suggest that where protected areas are smaller than the core zone of Cusuco National Park, mammal populations cannot be sustained and are vulnerable to local extirpation (Ortiz-Lozada et al. 2017).

Large mammal community composition of Cusuco National Park was comparable (taking into account species' known ranges) to those found in other Central American reserves (Thornton et al. 2011, Cove et al 2013, Tobler et al. 2008, Gonthier and Castañeda 2013) with the notable exception of Geoffroy's spider monkey and puma (Thornton et al. 2011, Tobler et al. 2008, Gonthier and Castañeda 2013), which were absent. Historical anecdotal evidence from interviews with local people (in the villages of Buenos Aires and Bañaderos) suggest Geoffroy's spider monkey was once present and indeed numerous but has not been seen for some time. The lack of records in Cusuco National Park suggests the species is now locally extirpated. Howler monkeys, by comparison, remain widespread in the park as they have a more adaptable diet and are less disturbed by forest fragmentation (Lenz et al. 2014) whilst becoming habituated to nearby human activity (McKinney et al. 2015). Moreover, their meat is reputed to have a bad flavor and they are not the focal target of hunting (pers. obs.). Anecdotal reports of puma remain unverified and they are known to avoid areas with human settlements (Foster et al. 2010).

It is noteworthy, that whilst ocelot tracks and signs have been detected within Cusuco National Park, no direct detections have been made via camera trapping. It is odd given the species' generally high abundance throughout Central and South America (Dillon and Kelly 2008, Davis et al. 2011), especially given that jaguar, a

Table 4. Non-volant mammalian species not detected in Cusuco National Park despite its inclusion within their IUCN range polygon. IUCN Red List codes: DD = Data deficient, LC = Least Concern, VU = Vulnerable and EN = Endangered (IUCN statuses extracted from http://www.iucnredlist.org, version 2016.3).

Species	Common name	IUCN status
PRIMATES		
Atelidae		
Ateles geoffroyi (Kuhl, 1820)	Geoffroy's spider monkey	EN
CARNIVORA		
Canidae		
Canis latrans (Say, 1823)	Coyote	LC
Felidae		
Puma concolor (Linnaeus, 1771)	Puma	LC
Mephitidae		
Spilogale angustifrons (Howell, 1902)	Southern spotted skunk	LC
RODENTIA		
Cricetidae		
Oryzomys couesi (Alston, 1877)	Coues' rice rat	LC
Ototylomys phyllotis (Merriam, 1901)	Big-eared climbing rat	LC
Sigmodon hirsutus (Burmeister, 1854)	Southern cotton rat	LC
Heteromyidae		
Heteromys salvini (Thomas, 1893)	Salvin's spiny pocket mouse	LC
PILOSA		
Cyclopedidae		
Cyclopes didactylus (Linnaeus, 1758)	Silky anteater	LC
Myrmecophagidae		
Myrmecophaga tridactyla (Linnaeus, 1758)	Giant anteater	VU
DIDELPHIMORPHIA		
Didelphidae		
Caluromys derbianus (Waterhouse, 1841)	Derby's woolly opossum	LC
Chironectes minimus (Zimmermann, 1780)	Water opossum	LC
Marmosa alstoni (J.A. Allen, 1900)	Alston's mouse opossum	LC
Philander opossum (Linnaeus 1758)	Gray four-eyed opossum	LC

generally rare big cat has been recorded on camera. Ocelot diet includes small mammals, birds and reptiles, but also includes larger sized prey (> 800 g) species, such as agoutis, armadillos and pacas (Sunquist and Sunquist 2002, Moreno et al. 2006, Bianchi et al. 2010); the latter of which is notably common in Cusuco National Park. It has also been shown to be present elsewhere in Honduras (Gonthier and Castañeda 2013).

Relative to other areas in Central America, we record notably low detection rates of agouti (Cove et al. 2013) which may be a consequence of hunting for bushmeat (Roger Alvarengo pers. comm.). However, unexpected low detections of the genus *Dasyprocta* by camera trapping has been shown elsewhere in South America despite high detection in transect surveys (Munari et al. 2011). However, the lack of agouti in Cusuco National Park as a prey base for ocelot may well help to explain the predator's absence as well.

Other mammal species may have gone unrecorded due to our sampling methods. For example, arboreal deployment of live traps would be required to record tree-living small mammals such as climbing rats (e.g. the big-eared climbing rat *Ototylomys phyllotis* Merriam 1901) or canopy dwelling species (for example, to confirm the presence of Geoffroy's spider monkey). Some species occupying habitats which are difficult to survey e.g. fossorial species like gophers or aquatic species that rarely leave the water's edge such as water mice (*Rheomys* sp.) may require focal sampling techniques.

A population viability model for Baird's tapir within Cusuco suggested that recent declines may lead to local extirpation (McCann et al. 2012). No evidence of tapir presence was detected in 2016 for the first time during annual surveys over the last decade, supporting the assertion that its population may indeed be reaching the lower threshold for detection. Moreover, the only evidence for the presence of the species detected since the completion of this survey, was a skeleton found during 2017 which showed signs that it had been hunted (pers. obs.).

During June 2016, a single jaguar was recorded for the first time within Cusuco National Park (Fig. 3P) in the "bosque enano" (dwarf forest) at 2,200 m above sea level (see https://www.panthera.org/blog/2016/06/15/surprise-2200-meters). Jaguars are typically associated with areas providing access to large-bodied prey; though in some regions such as Belize they may take smaller prey such as armadillos (Foster et al. 2010). In Cusuco National Park, prey likely includes tapir, red brocket, white-tailed deer, peccaries and conceivably domestic stock such as cattle in the north-west of the park, where deforestation

has given way to pockets of agriculture including pasture.

Conservation, both political lobbying and on-the-ground management, can only be effective with full knowledge of what species are present, their distribution and relative abundance. Here, we report a comprehensive species list of non-volant terrestrial mammals for Cusuco National Park including the presence of jaguar. Data on the impact of designation, disturbance and frequency of mammal detection may help to direct future conservation policy. We advise continued annual monitoring activity to provide a robust time-series, allowing temporal trends in occupancy and abundance to be investigated. Particular focus should be on those species vulnerable to exploitation for bushmeat by hunting as well as bioindicators such as top predators including jaguar. We also advise that consideration should be given to conducting an IUCN Regional Red Listing exercise (see http://www.iucnredlist.org/about/publication/regional-red-lists#Americas) for the mammals of Honduras.

Acknowledgements

We are grateful to all Operation Wallacea Ltd staff and students. We thank Mito, Roger and Lucas whose local knowledge and species identification skills were invaluable. Annual contributions to the sightings database were contributed to by (listed in alphabetical order of surname): Alexandra Andino, Mandy Apps, Sara Aubery, David Beaune, Julie Boudreau, Marcella Chelli Nuzzo, Ruth Cox, Augusta Dorey, Ryan Gardiner, Guillermo Fandos Guzman, Rachael Forster, Abi Harrison, Karen Hornigold, Sam Jones, Martha Nash, Steven MacKenzie, Rebecca McGowan-Griffin, Eric McNeill, Luke Nichols, Charlotte Palmer, Sara Paul, Nick Pruijn, Sam Puls, Dario Rivera, Scott Schilds, Sarah Sells, Nina Storm, Sam Stubbs, Ben Wallis, Phil Wheeler, Geoff While, Clare Wilkinson, Katy Wilson, CB Woods and Amelia Zakiewicz. We acknowledge the Instituto de Conservación Forestal (ICF), who maintain the Base camp facilities. We are particularly grateful to Roberto Downing from Expediciones y Servicios Ambientales de Cusuco (ESAC) without whom fieldwork would not have been logistically possible. The primary author was supported by funding from the Department for Employment and Learning, Northern Ireland (http://www.delni.gov.uk). We are grateful to Dr Sarah Helyar for the use of her laboratory to conduct molecular genetic analysis for shrew identification. Thanks to Georg Hantke, Curatorial Preparator and Dr Andrew Kitchener, Principal Curator of Vertebrates in the Department of Natural Sciences for preparing and lodging *Cryptosis* shrew specimens in the National Museum of Scotland, Edinburgh, facilitating species identification. We thank Michael Cove, editor William Corrêa Tavares and another anonymous reviewer for their helpful feedback.

Authors' contributions

HH was the primary author, OB built and maintained the database of records, KD performed molecular genetic analyses on Crytotis spp, KS and NMcC led much of the data collection and coordination, MJ conceived of the study, FC led data collection for Panthera and NR was the primary supervisor. All authors were involved in data collection and read, edited and approved the manuscript.

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Appendix

Camps surveyed for small mammals

	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Buenos Aires	Y	Y	Y	Y	Y	N	N	Y	Y	N	N
Base camp	Y	Y	Y	Y	Y	N	Y	Y	Y	Y	Y
Cantiles	Y	Y	Y	Y	N	N	N	Y	Y	Y	Y
Cortecito	Y	Y	Y	N	N	N	Y	Y	Y	Y	Y
Danto	Y	Y	Y	N	N	N	N	Y	Y	Y	Y
Guanales	Y	Y	Y	N	N	N	N	Y	Y	Y	Y
Santo Tomas	N	Y	Y	N	N	N	N	Y	Y	Y	N

Total line transect km per camp each year

	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Base camp	8.5	0	16.9	20	12.7	14.8	14.8	14.8	7.4	9.2	7.4
Buenos Aires	0	0	12.88	5.94	11.88	11.88	11.88	5.94	5.94	0	0
Cantiles	18.7	7.4	21.1	14	13.2	13.2	13.2	6.6	6.6	6.6	6.6
Cortecito	35	22.3	21.4	8.7	17.4	17.4	16.4	8.7	7.7	6.7	6.7
Danto	23.4	17.7	18.6	15.2	18.6	13.4	15	9.3	14.6	7.3	7.3
Guanales	22.79	13.03	13.46	10.43	14.09	13.46	13.46	6.73	6.73	6.73	6.73
Santo Tomas	0	0	8.74	4.37	5.94	8.37	7.64	4.37	0	0	0

Camera trapping placement per camp

	2014	2015	2016
Base Camp	8	24	20
Buenos Aires	4	0	0
Cantiles	5	23	21
Cortecito	6	16	17
Danto	11	22	18
Guanales	8	20	18